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Growth Characteristics of Intertidal Limpets in Relation to Temperature Trends[1]

RON KENNY[2]

ABSTRACT: Three species of the intertidal limpet genus *Cellana* are distributed along the east coast of Australia in a latitudinal sequence. Collections of limpets were made at eight localities spanning 27 degrees of latitude. Shell length measurements were analyzed to establish growth constants and these constants were related to environmental temperatures. The most southerly population showed a marked reduction in growth rate. Growth rates at the tropical and warm temperate locations form a sequence in which the growth constants (relative to temperature) of the tropical species change more markedly than do those of the temperate species.

SEVERAL REVIEWS have discussed the literature concerning the distribution and physiology of organisms relative to latitude and temperature (Scholander et al. 1953, Bullock 1955, Dehnel 1955, Prosser 1958, Segal 1961, Vernberg 1962, Vernberg and Vernberg 1970). In particular, several studies of molluscan shell growth and calcification relative to temperature have been reported (Newell 1964, Wilbur and Owen 1964). In some of these studies, geographically differing populations of a single species have been used (Swan 1952, Dehnel 1956, Taylor 1959, 1960); in other cases latitudinal or temperature influences have been assessed by comparing growth characteristics of several species (Dehnel 1955, Graus 1974). In general such investigations have been carried out in temperate or cool water areas (Newell 1964, Wilbur and Owen 1964), although Graus (1974) studied mollusks from tropical, subtropical, and cool temperate regions.

On the east coast of Australia there are three intertidal species of limpets in the genus *Cellana*. These three species, each occurring in similar mid-littoral situations (Dakin, Bennett, and Pope 1948, Bennett and Pope 1953, Endean, Kenny, and Stephenson 1956, Bennett and Pope 1960), are distributed in a latitudinal sequence along the coast. Details of the geographical distribution are given by the above authors and summarized by Macpherson (1955), Guiler (1960), and Knox (1963). *Cellana conciliata* Iredale, 1940 is found along the Queensland coast north from approximately latitude 26° S. In southern Queensland and along the coasts of New South Wales and Victoria *C. tramoserica* (Chemnitz), 1795 (refigured by Sowerby, 1825) is present. *C. solida* (Blainville), 1825 occurs on the Tasmanian coast and in some areas on the Bass Strait coast of Victoria (Figure 1).

The three species, ranging through approximately 30 degrees of latitude from tropical to cool temperate biogeographic provinces (Knox 1963), form a suitable study group for an investigation of latitudinal and temperature influenced trends in molluscan shell growth.

METHODS

Random collections of limpets were made throughout the intertidal distribution of the *Cellana* species at eight localities from Cooktown (lat 15°28′ S) to Blackman's Bay (lat

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[2] James Cook University of North Queensland, Department of Zoology, School of Biological Sciences, Townsville, Queensland, 4811 Australia.

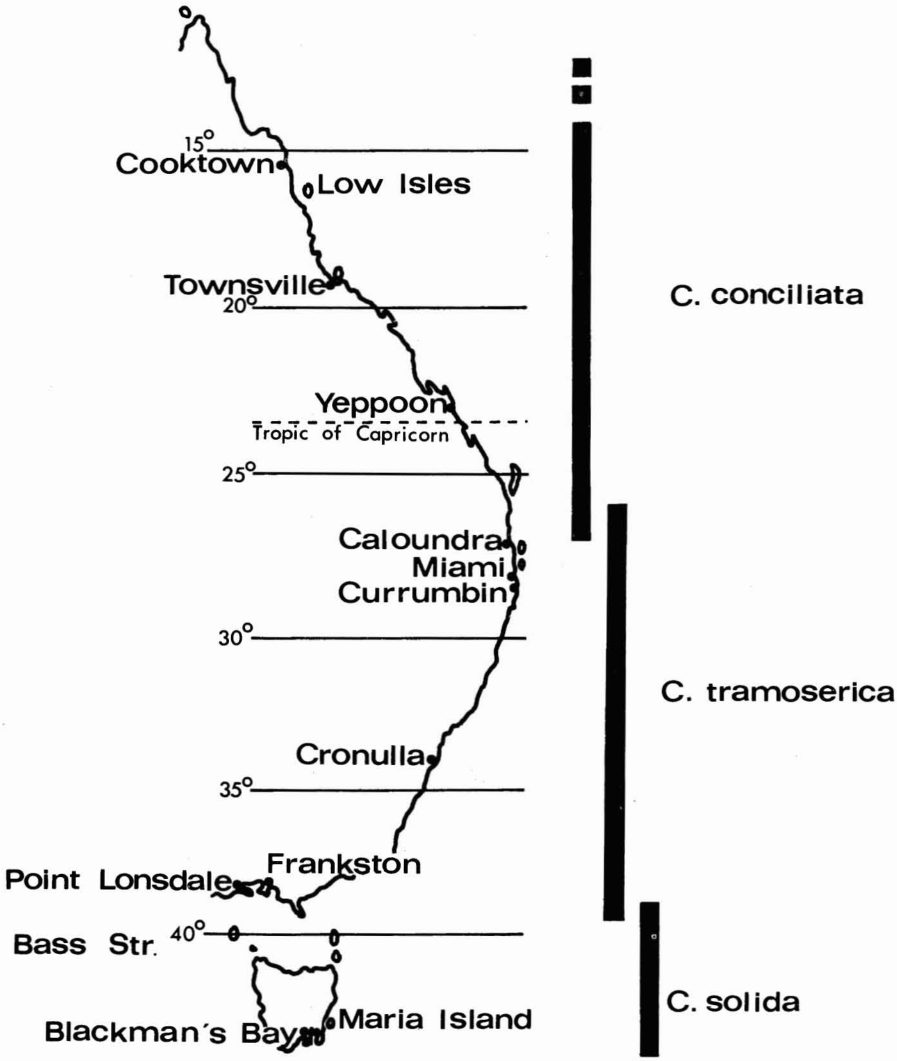

FIGURE 1. Distribution of three species of *Cellana* on the east coast of Australia and location of places mentioned in the text.

42°55′S) (Table 1 and Figure 1). All collections were made during January to eliminate the possibility of differences due to seasonal variability in growth.

Measurements of total shell length were recorded to the nearest 0.1 mm with vernier calipers. The conical rather than helical shape of the limpet shell permits the use of a linear measurement to describe growth. Linear dimensions have been used to establish growth constants in gastropod larvae (Dehnel 1955); bivalve mollusks (Swan 1952, Dehnel 1956, Taylor 1959, 1960, Wilbur and Owen 1964) and in limpets (Kenny 1969, 1977). The data were arranged in length frequency classes (Figure 2). In the absence of easily recognizable shell markings designating year classes (Wilbur and Owen 1964, Kenny 1969), these polymodal distributions were analyzed using the methods devised by Harding (1949) and elaborated by Cassie (1950, 1954). The resultant class size mean values were used to

TABLE 1

Temperatures and Limpet Growth Constants

		Temperature°C							
LOCALITY	LATITUDE S	MAX.	MIN.	MIDPOINT	N_1*	AUTHORITY	SPECIES	N_2†	GROWTH CONSTANT
Cooktown	15°28′	—	—	—	—	—	*C. conciliata*	113	0.58
Low Isles	16°23′	29.8	22.0	25.9	349	Moorhouse (1933)	—	—	—
Townsville	19°15′	31.2	21.8	26.5	212	Kenny (1974)	*C. conciliata*	198	0.54
Yeppoon	23°08′	27.5	18.4	23.7	48	Ms records	*C. conciliata*	169	0.64
Caloundra	26°48′	26.8	18.4	22.6	38	Ms records	*C. tramoserica*	121	0.69
Miami	28°07′	26.0	19.1	22.5	24	Ms records	—	—	—
Currumbin	28°09′	—	—	—	—	—	*C. tramoserica*	175	0.66
Cronulla	34°04′	22.8	16.1	19.4	108	CSIRO Australia (1956, 1957*a*, 1957*b*)	*C. tramoserica*	118	0.71
Frankston	38°00′	—	—	—	—	—	*C. tramoserica*	136	0.75
Pt. Lonsdale	38°18′	19.4	11.3	15.4	cont‡	King (1970)	—	—	—
Maria Island	42°40′	16.7	11.1	13.9	21	CSIRO Australia (1963) and Rotchford (1975)	—	—	—
Blackman's Bay	42°55′	—	—	—	—	—	*C. solida*	94	0.92

Note: Specimen collections were made at locations near but not identical with those for temperature data.
* N_1 number of temperature readings.
† N_2 number of limpets collected.
‡ Continuous recording.

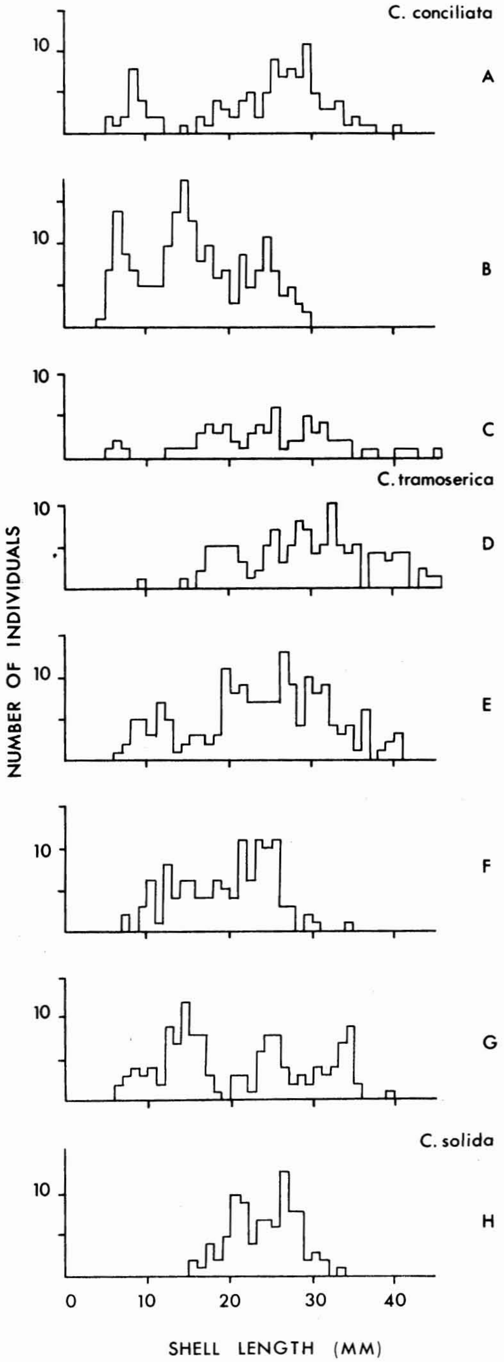

FIGURE 2. Shell length frequency distributions from collections of three *Cellana* species. Locations of collection: *a*, Cooktown; *b*, Townsville; *c*, Yeppoon; *d*, Caloundra; *e*, Currumbin; *f*, Cronulla; *g*, Frankston; *h*, Blackman's Bay.

estimate growth curves for the eight populations sampled. Manuscript records from field growth studies of *C. solida* (H. Dudgeon, personal communication) and *C. conciliata* (Kenny, field notes) and statements by Parry (1978) for *C. tramoserica* support the calculated growth curves.

To compare the growth curves, linear transformations were calculated using the methods outlined by Walford (1946) and discussed by Hancock (1965). From these transformations, growth constants for the relationship between shell length and age were established for each population (Walford 1946). It should be noted that these "transformation constants" are not the equivalent of the "relative growth constant" (Wilbur and Owen 1964), and here a smaller value of the constant signifies a more rapid rate of growth.

Sea temperature data were collected from published and manuscript records for selected localities ranging from Low Isles (lat 16°23′ S) to Maria Island (lat 42°40′ S) (see Table 1). As the number of records and regularity of sampling varied for different localities, the midpoint of the range, rather than the mean, was used to establish a relationship between water temperature and latitude. For each locality midsummer and midwinter records were available. The growth constants calculated for each of the populations of *Cellana* species were related to sea temperatures.

RESULTS

The relationship between latitude and temperature is linear (Figure 3) and can be described by the equation

$$\text{Temperature } ^\circ\text{C} = 0.488 \text{ (latitude)} + 35.17$$

Bennett and Pope (1953) have commented that sea temperatures in Bass Strait may be lower than expected for the particular latitude, but the present data from coastal localities suggest a consistent relationship between latitude and temperature.

The transformation growth constants calculated from the shell measurements ranged from a minimum value of 0.54 (largest growth rate) for a northern population to 0.92 (small-

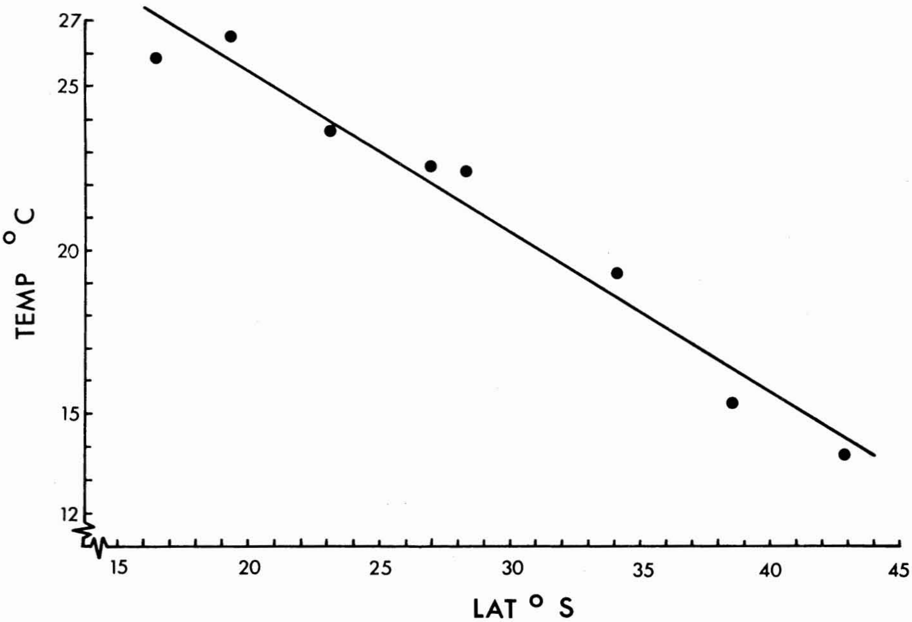

FIGURE 3. Relationship between latitude (degrees south) and the midpoint of the annual sea temperature range.

est growth rate) for the most southern population (Table 1).

The simplest interpretation of these values in relation to the sea temperature data is as separate linear equations for *C. conciliata* and *C. tramoserica* (Figure 4). As there were only three samples for *C. conciliata*, alternative relationships could be postulated.

The calculated equations are:

C. conciliata: growth constant = -0.037 (temperature) $+ 1.52$
C. tramoserica: growth constant = -0.011 (temperature) $+ 0.92$

The rate of growth for populations of these *Cellana* species decreases (increasing transformation growth constant) at lower temperatures. The northern populations of *C. tramoserica* show growth constants similar to those of *C. conciliata* at similar temperatures; but the slope of the equation for *C. tramoserica* is reduced, indicating that the change in growth rate with decreasing environmental temperatures is less for this species than for the northern species, *C. conciliata* (Figure 4).

The data for the single collection of *C. solida* show a slower growth rate (larger transformation growth constant) than those for the other species.

DISCUSSION

Studies comparing the growth of Californian and Alaskan bivalves show a decrease in growth rate at higher latitudes or with a decrease in temperature (Dehnel 1956, Taylor 1959, 1960). Swan (1952), discussing the effects of localized environmental factors on the growth of a bivalve mollusk, concluded that growth was slower at northern (colder) localities. Other molluscan examples of this latitudinal influence on growth are listed by Newell (1964). Both *C. conciliata* and *C. tramoserica* conform to this pattern.

The linear relationships between the growth constant and temperature for two of the Australian limpet species through a temperature range of 15° to 26°C show a change of slope (increased growth rate relative to temperature) from the tropical species (*C. conciliata*) to the warm temperate species (*C. tramoserica*) (Figure 4). This contrasts with the

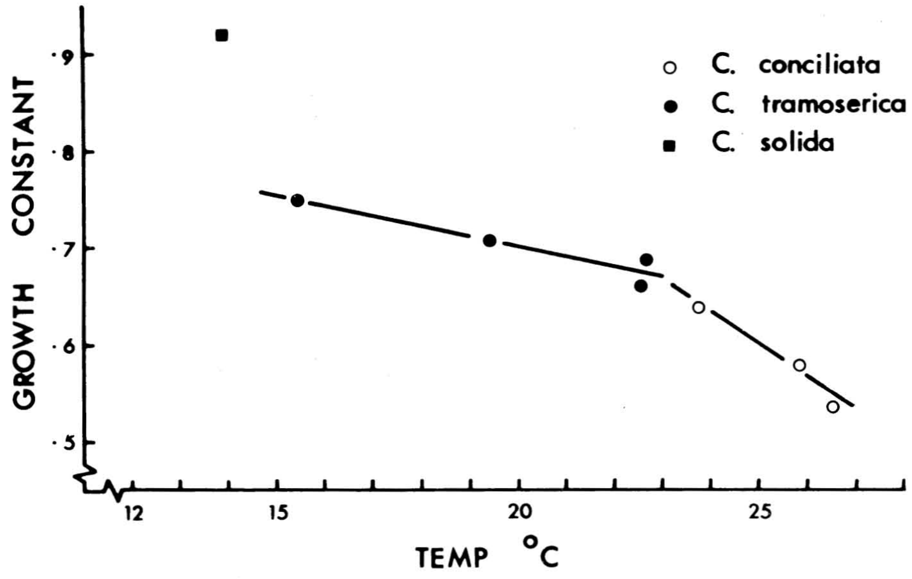

FIGURE 4. Relationship between the midpoint of the annual sea temperature range and the shell length growth constant for three species of *Cellana*.

straight regression line relating calcification indices to temperatures from 9° to 27°C for several North Atlantic mollusks (Graus 1974).

The growth constant–temperature relationship for the Tasmanian population (*C. solida*) differs markedly from the calculated regression line for the warm temperate species (Figure 4), suggesting that between latitudes 38° and 42° S there is a change in the growth characteristics of the limpets, resulting in a reduction of growth rate even though the environmental temperature is lowered only 1.5°C (Table 1). Graus (1974) also recorded a marked change in growth index for several North Atlantic gastropods between latitudes 35° and 40° N. The value of the growth constant–temperature relationship for *C. solida* falls near an extrapolation from the regression line calculated for *C. conciliata* (Figure 4), matching the Graus (1974) single-growth index relationship through a wide range of temperatures. This suggests that the warm temperate species *C. tramoserica* is anomalous in maintaining a greater growth rate than expected at lower temperatures (Figure 4).

Segal (1961) and Vernberg (1962) have listed examples of matching intraspecific growth rates from geographically separated populations with different temperature regimes, that is, showing a "compensation pattern" relative to temperature. Dehnel (1955) showed that for four species of gastropods, larval growth was influenced by a similar effect, growth being relatively more rapid in Alaskan than Californian populations. The warm temperate species *C. tramoserica* shows a similar pattern, with relatively small differences between the growth constants associated with decreasing environmental temperatures through its distribution range.

The geographic range of *C. tramoserica* conforms to the geographic region designated "warm temperate and transitional" (Bennett and Pope 1953, Knox 1963). This distribution is associated with a wider temperature gradient than applies to the tropical species (Table 1) and thus may influence the intraspecific growth variability.

Vernberg (1962) has suggested that the wider fluctuations of environmental temperatures of the temperate zone in contrast to the tropics are significant in establishing varied temperature-influenced physiological patterns in temperate zone animals. This pattern applies to a comparison of the tropical and temperate species of *Cellana*, with *C. tramoserica* exhibiting an altered growth constant–temperature relationship relative to the other species.

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